Corrections

PHARMACOLOGY

Correction for “Selective activation of the M_1 muscarinic acetylcholine receptor achieved by allosteric potentiation,” by Lei Ma, Matthew Seager, Marion Wittmann, Marlene Jacobson, Denise Bickel, Maryann Burno, Keith Jones, Valerie Kuzmick Graufelds, Guangping Xu, Michelle Pearson, Alexander McCampbell, Renee Gaspar, Paul Shughrue, Andrew Danziger, Christopher Regan, Rose Flick, Danette Pascarella, Susan Garson, Scott Doran, Constantine Kreatsoulas, Lone Veng, Craig W. Lindsley, William Shipe, Scott Kuduk, Cyrille Sur, Gene Kinney, Guy R. Seabrook, and William J. Ray, which appeared in issue 37, September 15, 2009, of *Proc Natl Acad Sci USA* (106:15950–15955; first published August 26, 2009; 10.1073/pnas.0900903106).

The authors note that the author name Matthew Seager should have appeared as Matthew A. Seager. The online version has been corrected. The corrected author line and related footnotes appear below.

Lei Ma[1], Matthew A. Seager[1], Marion Wittmann[1], Marlene Jacobson, Denise Bickel, Maryann Burno, Keith Jones, Valerie Kuzmick Graufelds, Guangping Xu, Michelle Pearson, Alexander McCampbell, Renee Gaspar, Paul Shughrue, Andrew Danziger, Christopher Regan, Rose Flick, Danette Pascarella, Susan Garson, Scott Doran, Constantine Kreatsoulas, Lone Veng, Craig W. Lindsley, William Shipe, Scott Kuduk, Cyrille Sur, Gene Kinney, Guy R. Seabrook, and William J. Ray

Author contributions: L.M., M.A.S., M.W., M.J., A.M., P.S., C.R., S.D., C.K., C.S., G.K., and W.J.R. designed research; L.M., M.A.S., M.W., D.B., M.B., K.J., V.K.G., G.X., M.P., A.M., R.G., A.D., R.F., D.P., S.G., C.K., L.V., and W.S. performed research; M.J., C.W.L., W.S., and S.K. contributed new reagents/analytic tools; L.M., M.A.S., M.W., M.J., A.M., P.S., C.R., S.D., C.K., L.V., C.W.L., S.K., C.S., G.K., G.R.S., and W.J.R. analyzed data; and W.J.R. wrote the paper.

[1] L.M., M.A.S., and M.W. contributed equally to this work.

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ANTHROPOLOGY

Correction for “Additional evidence on the use of personal ornaments in the Middle Paleolithic of North Africa,” by Francesco d’Errico, Marian Vanhaeren, Nick Barton, Abdeljalil Bouzouggar, Henk Mienis, Daniel Richter, Jean-Jacques Hublin, Shannon P. McPherron, and Pierre Lozouet, which appeared in issue 38, September 22, 2009, of *Proc Natl Acad Sci USA* (106:16051–16056; first published August 28, 2009; 10.1073/pnas.0903532106).

The authors note that Abdeljalil Bouzouggar should be credited for designing and performing the research. The corrected author contributions footnote appears below.

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PERSPECTIVE

Correction for “Feeding aquaculture in an era of finite resources,” by Rosamond L. Naylor, Ronald W. Hardy, Dominique P. Bureau, Alice Chiu, Matthew Elliott, Anthony P. Farrell, Ian Forster, Delbert M. Gatlin, Rebecca J. Goldburg, Katheline Hua, and Peter D. Nichols, which appeared in issue 36, September 8, 2009, of *Proc Natl Acad Sci USA* (106:15103–15110; first published September 8, 2009; 10.1073/pnas.0905235106).

The authors note that an additional institutional affiliation should be listed for author Ian Forster: Oceanic Institute, 41-202 Kalanianaole Highway, Waimanalo, HI 96795. The corrected author line, affiliation line, and a related footnote appear below.

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APPLIED PHYSICAL SCIENCES

Correction for “High-sensitivity microfluidic calorimeters for biological and chemical applications,” by Wonhee Lee, Warren Fon, Blake W. Axelrod, and Michael L. Roukes, which appeared in issue 36, September 8, 2009, of *Proc Natl Acad Sci USA* (106:15225–15230; first published August 24, 2009; 10.1073/pnas.0901447106).

The authors note that, due to a printer’s error, on page 15227, right column, the equation on lines 14 and 15 of the first full paragraph appeared incorrectly. This error does not affect the conclusions of the article. The corrected equation appears below.

$$E = \int_0^{t_\mathrm{m}} GV(t)/S\ dt$$

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PERSPECTIVE

Feeding aquaculture in an era of finite resources

Rosamond L. Naylor[a,1], Ronald W. Hardy[b], Dominique P. Bureau[c], Alice Chiu[a], Matthew Elliott[d], Anthony P. Farrell[e], Ian Forster[e], Delbert M. Gatlin[f,g], Rebecca J. Goldburg[h], Katheline Hua[c], and Peter D. Nichols[i]

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Edited by Thomas F. Malone, North Carolina State University, Raleigh, NC, and approved July 17, 2009 (received for review May 18, 2009)

Aquaculture's pressure on forage fisheries remains hotly contested. This article reviews trends in fishmeal and fish oil use in industrial aquafeeds, showing reduced inclusion rates but greater total use associated with increased aquaculture production and demand for fish high in long-chain omega-3 oils. The ratio of wild fisheries inputs to farmed fish output has fallen to 0.63 for the aquaculture sector as a whole but remains as high as 5.0 for Atlantic salmon. Various plant- and animal-based alternatives are now used or available for industrial aquafeeds, depending on relative prices and consumer acceptance, and the outlook for single-cell organisms to replace fish oil is promising. With appropriate economic and regulatory incentives, the transition toward alternative feedstuffs could accelerate, paving the way for a consensus that aquaculture is aiding the ocean, not depleting it.

aquafeed | fish oil | fishmeal | forage fish

Aquaculture is set to reach a landmark in 2009, supplying half of the total fish and shellfish for human consumption (ref. 1 and www.fao.org/fishery/statistics/software/fishstat/en). With the production of farmed fish eclipsing that of wild fish, another major transition is also underway: aquaculture's share of global fishmeal and fish oil consumption more than doubled over the past decade to 68% and 88%, respectively (2).[*] This trend reflects rapid growth in aquaculture production and decreased use of fishmeal in the livestock sector in response to higher prices, but it belies significant improvements in aquaculture feed efficiencies that have occurred simultaneously. Impressive gains have been achieved in reducing feed conversion ratios (FCRs) for piscivorous fish and in substituting nonfish ingredients into formulated feeds. The volume of omnivorous species production has also risen, as seen, for example, in the transition in Asian shrimp farming from *Penaeus monodon* (piscivorous) to *Litopenaeus vannamei* (omnivorous). The ratio of wild fish input via industrial feeds to total farmed fish output (excluding filter feeders) has fallen by more than one-third from 1.04 in 1995 to 0.63 in 2007 (see Fig. S1), a decline that underscores the expanding volume of omnivorous fish produced on farms and market pressures to reduce fishmeal and fish oil levels in aquafeeds. Nonetheless, serious challenges remain for lowering the aggregate level of fishmeal and fish oil inputs in feeds and alleviating pressure on reduction fisheries over time (see *SI Text*). Volatile commodity markets have disrupted the orderly transition in feed ingredient substitution, and consumers increasingly favor products high in long-chain (LC) omega-3 fish oil content for health reasons.[†]

Here, we examine the use of fishmeal and fish oil in industrial aquafeeds and alternative nonforage fish ingredients and ask: What are the constraints on and opportunities for further reducing aquaculture's dependence on wild fisheries? This question is gaining relevance on many fronts and with numerous audiences. With the current economic downturn, aquaculture producers are seeking to reduce costs, and feeds typically represent the largest variable cost in their budgets. At the same time, consumers are seeking to purchase animal protein with high health benefits and low health risks from contaminants such as polychlorinated biphenyls (PCBs) and dioxins, sometimes associated with fishmeal and fish oil use. In addition, consumers and retailers have become increasingly interested in sustainability metrics, including the ratio of wild fisheries inputs to farmed fish outputs or the "fish-in to fish-out" ratio (FI/FO) for farmed seafood. Indeed, to encourage the development of nonfish alternatives, the National Organics Standards Board (NOSB) recently proposed limiting the use of fishmeal and fish oil in organically certified aquaculture products with a 12-year phase-out schedule (4). And finally, on the policy front, legislation enacted in California (the Sustainable Oceans Act, SB 201) and a bill introduced at the United States federal level (the National Offshore Aquaculture Act of 2007, H.R. 2010 and S. 1609) incorporate language to minimize the use of fishmeal and fish oil in feeds. Even so, the regulatory measures needed to implement such language remain unclear.

The goal of this analysis is to illuminate the future path of feeds for producers, consumers, processors, retailers, and policymakers by evaluating the use of fish and nonfish alternatives. Given the significant quantities of fishmeal used to feed terrestrial animals (mainly swine and poultry), we also examine the relative efficiencies of protein conver-

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The authors declare no conflict of interest.

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[*] We have chosen to use new fish feed data from ref. 2, which come from the Food and Agriculture Organization, the International Fishmeal and Fish Oil Organization (IFFO), and a global survey of feed manufacturers, farmers, researchers, fisheries specialists, and other stakeholders in 50 countries from December 2006 to October 2007. These numbers differ from IFFO fishmeal and fish oil data, which come from sales data and thus likely underestimate total use.

[†] We use the term LC omega-3s to refer to the beneficial n-3 LC ($\geq C_{20}$) polyunsaturated fatty acids (LC-PUFA), which are comprised mainly of eicosapentaenoic acid (20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3) (3).

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Table 1. Feed use and efficiencies (1995 and 2007)

Species group	Percentage on feeds*	Average FCR[†]	Average % fishmeal in feed[‡]	Average % fish oil in feed[‡]	Total feeds used[§]
Shrimp					
1995	75	2.0	28	2	1,392
2007	93	1.7	18	2	5,603
Salmon					
1995	100	1.5	45	25	806
2007	100	1.3	24	16	1,923
Marine fish					
1995	50	2.0	50	15	498
2007	72	1.9	30	7	2,311
Chinese carp (nonfilter feeding)					
1995	20	2.0	10	0	1,970
2007	47	1.7	5	0	8,578
Tilapia					
1995	70	2.0	14	1	984
2007	82	1.7	5	0	3,590

Data are from ref. 2.

*Estimated percentage of total species-group production fed on compound aquafeeds.

[†] Estimated average species-group economic FCR (total feed fed/total species group biomass increase), also known as EFCR.

[‡] Also known as fish inclusion rates.

[§] Total compound aquafeeds used for species group (thousand tons).

sion for aquaculture and livestock production. Searching for alternatives to fish-based feeds in an increasingly integrated world food system presents some tough choices. For example, is the use of rendered animal products (e.g., feather meal, bone meal, blood meal) preferable to fishmeal as a protein source for farmed fish? Are genetically modified vegetable oils that provide LC omega-3 oils an acceptable substitute for fish oil? How should forage fish resources be allocated among competing uses: to the highest economic value (e.g., ranched bluefin tuna), to feeding the largest number of people, or to conserving natural ecosystems? What criteria should be used to assess the ecological effects of using forage fish for feeds? Answers to these questions will ultimately determine aquaculture's future impact on forage fisheries.

Marine Resource Utilization

Most forage fisheries are either fully exploited to overexploited or are in the process of recovering from overexploitation (5). Production is also affected by substantial climate-induced variation (El Niño-Southern Oscillation events), particularly in the eastern Pacific (Peru, Chile). For several decades, 20 million to 30 million metric tons (mmt) of reduction fish (1/4 to 1/3 of the global fish catch) have been removed from the marine food web each year to produce fishmeal and fish oil for animal feeds and other industrial purposes (1). Another 5.6–8.8 mmt (mean of 7.2 mmt) of "low value/trash fish" and other forage fish are used for nonpelleted (farm-made) aquafeeds (6). In natural systems, forage fish play an important role in converting plankton into food for higher trophic-level species including humans, larger fish, marine mammals, and seabirds (7). Overexploitation of forage fisheries can lead to local stress on these higher trophic species, particularly during El Niño events (8, 9).

For the past few decades, the annual global production of fishmeal and fish oil has remained relatively steady at ≈5–7 mmt of fishmeal and 0.8–1.5 mmt of fish oil (10). Chile and Peru account for ≈40% of total production (10). Patterns of growth and globalization of fishmeal trade have been tied to changes in the aquaculture industry (11, 12). Aquaculture-producing countries such as Thailand, Chile, and China are consuming greater amounts of domestic fishmeal supplies, exporting lower volumes of feed, and importing fishmeal from other countries (12). More than half of Peru's and Chile's fishmeal exports now go to three Asian countries: China, Japan, and Taiwan. Asia is the largest global consumer of fishmeal overall (57%), with China accounting for half of the regional total (1). Asia is also the main user of trash fish for aquaculture production, with China's consumption alone estimated at 4–5 mmt in 2005 (6). Consumption of fish oil, used most heavily in salmon production, remains dominated by Europe (50%).

Farmed production of fish and shellfish nearly tripled in volume between 1995 and 2007. Despite marked improvements in FCRs and reductions in fishmeal and fish oil inclusion rates (percentage of fishmeal and fish oil in feeds), demand for fish inputs by the aquaculture sector increased. Aquaculture's consumption of fishmeal almost doubled to 3.6 mmt, and fish oil use grew by two-thirds to 835,000 mt (2). One factor contributing to this growth was that the share of farmed fish produced by using compound feeds rose for virtually all species (Table 1). Almost half of Chinese carp, >80% of tilapia, and 93% of shrimp in aquaculture systems are now raised on compound feeds to some extent. Although fishmeal inclusion rates are low for the omnivorous species, total production volumes, and thus fishmeal volumes, are large. In addition, 1995–2007 saw higher than average growth rates in the marine fish sector. Farmed marine fish have higher average FCRs and fishmeal inclusion in their diets.

Two main concerns arise from aquaculture's increasing share of fishmeal and fish oil consumption given the finite nature of global marine resources. The first issue is that, because of challenges in finding suitable substitutes, fishmeal and fish oil demand by aquaculture is less responsive to prices than demand by the livestock industry (13). Thus, unless appropriate substitutes are found, growth in the aquaculture sector is likely to push prices for the relatively fixed level of fishmeal and fish oil production higher. Higher commodity prices can create incentive for overfishing in poorly regulated fisheries or economically marginal fisheries. The second concern is that globalization of fishmeal and fish oil trade has resulted in lower traceability of the origin of feed and hence reduced accountability by feed consumers for the pressure they place on specific forage fisheries. As Deutsch et al. (12) note, there is limited feedback between the economic performance of aquaculture producers and the impacts that the industry has on the marine ecosystems that supply them.

Feed Efficiencies in Aquaculture and Livestock Production

Reducing aquaculture's dependence on marine resources in the future will depend on improving feed efficiencies and substituting away from fishmeal and fish oil. The FCRs and feed inclusion rates presented in Table 1 represent averages for the industry, but a wide variation exists among production systems within and among countries for any given species, year, and point in the farmed species' life cycle. Feed inclusion rates in 2006 were documented to vary by as much as 63% for fishmeal and up to 26% for fish oil (see Table S1). Similarly, reported FCRs in 2006 ranged

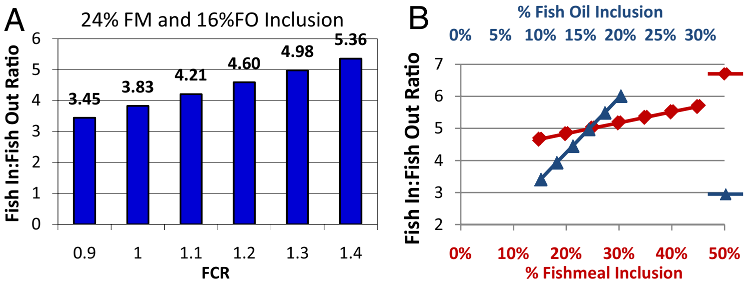

Fig. 1. Sensitivity of FI/FO to changes in FCRs (*A*) and fishmeal and fish oil inclusion rates (*B*). Base assumptions for FCR and fishmeal and fish oil inclusion in diets ($Incl_{FM}$, $Incl_{FO}$) are taken from Table 1. FI/FO represents kg of reduction fish required to produce 1 kg of farmed fish, equal to the sum of the reduction fish equivalent for fishmeal (RFE_{FM}) and additional fish oil (RFE_{AO}). RFE_{FM} is calculated as: FCR × $Incl_{FM}/0.225$, assuming that the average yield of 1-kg reduction fish made into fishmeal is 22.5%. In calculating RFE_{AO}, residual fish oil and the amount of oil extractable from RFE_{FM} are both subtracted from the total fish oil inclusion. It is assumed that 8% residual fish oil on average is found in fishmeal. Hence RFE_{AO} is: $[FCR \times (Incl_{FO} - 0.08 \times Incl_{FM})/0.05] - (0.05 \times RFE_{FM})$, where the average yield of 1-kg reduction fish made into fish oil is assumed to be 5%. Original calculations by R.W.H. in 2008.

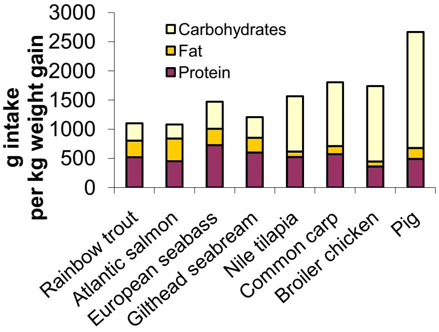

Fig. 2. Comparison of macronutrient intakes required for producing 1 kg of biomass gain in different fish and livestock (pig, broiler chicken) species based on feed practices in 2007. These data are based on D.P.B. and K.H.'s original calculations from information obtained directly from industry sources and expert knowledge of feed practices (feed inputs, conversion ratios) during the entire life cycle of each species. The calculations represent commercial (not experimental) practices under normal operating conditions averaged across the industry. This average incorporates differences in regulatory environments, final market weights, ingredient prices, and production constraints such as disease. The calculations show g of macronutrient intake per kg of farmed weight gain. They include the whole animal and do not separate out the edible portions, the latter being too variable for this analysis.

from 1.0 to 2.5 for shrimp, 1.0 to 1.6 for salmon, and 1.0 to 2.6 for tilapia (2). Determining which FCRs and inclusion rates are most representative ultimately dictates the FI/FO calculation for any particular species.

Moreover, different species vary considerably in the extent to which FCRs and the inclusion of fishmeal and fish oil in their diets affect FI/FO ratios. Taking farmed Atlantic salmon as an example of an industry highly reliant on fishmeal and fish oil, an improvement in the FCR from 1.4 to 1.0 leads to a FI/FO of 5.4 versus 3.8 (Fig. 1*A*). The FI/FO for farmed salmon, currently at 5.0, is much more sensitive to changes in fish oil inclusion than fishmeal inclusion (Fig. 1*B*). Reducing fish oil content by 4% leads to a decline in FI/FO from 5.0 to 3.9; by contrast, changing fishmeal use by 4% from current rates has a much more moderate impact on FI/FO (5.0 versus 4.8). In other words, the amount of forage fish used to produce feeds for salmon is driven by the need for fish oil to a far greater extent than fishmeal (see Fig. S2 for complete analysis of fishmeal and fish oil inclusion combinations). The converse is true of shrimp and Chinese catfish culture, in which the use of industrial fish products is driven by the need for fishmeal.

Calculating FI/FO ratios is complicated by the fact that feeds for some species, like salmon and trout, are high in fish oil, whereas feeds for other species, such as tilapia and carp, contain fishmeal but very little fish oil. For salmonid species, the essential n-3 LC-PUFA requirement exceeds that supplied by residual oil in fishmeal if dietary fishmeal levels are <40%. However, more fish oil is used in salmonid diets to ensure healthful n-3 LC-PUFA levels in fillets. The additional forage fish needed for the extra oil creates a high FI/FO (Fig. 1*B*). Alternatively, if one assumes no excess requirement for fish oil and both ingredients are treated equally in the calculation, then FI/FO would be lower.[‡] The latter assumption allows one to add up all species to reach a grand total, because excess fishmeal or fish oil from the diet of any given species will be consumed ultimately by other fish or livestock species, or even by humans in the case of residual fish oil. However, such a calculation obscures the fact that rising demand for species high in fish oil could lead to continued increases in the amount of forage fish used in feeds. In other words, consumers' expanding appetite for LC omega-3s has the potential to drive up demand for forage fish in feeds over time unless substitute forms of oil are used (see *SI Text*).

Our analysis underscores that improvements in FCRs and inclusion rates ultimately lead toward more efficient use of marine resources. In evaluating efficiencies, however, it is important to extend the comparison for aquatic farmed species to terrestrial farmed species (Fig. 2) because aquaculture and livestock draw on the same set of nutrient sources. Three macronutrients (protein, lipid, and carbohydrate) are necessary for both animal and human nutrition. Starch and lipids are also used by the biofuels sector to produce ethanol and biodiesel, respectively (14).

The protein requirement, which is primarily used for tissue growth, varies little among farmed species. Even so, the origins of proteins in animal feeds vary widely (see Fig. S3), with marine piscivorous species such as European seabass and gilthead seabream most dependent on fishmeal for protein (>40% inclusion). Fishmeal also represents a significant (20–55%, depending on life history stage), but declining, contribution to total protein intake in rainbow trout and Atlantic salmon. In contrast, cereal and oilseed proteins play a much larger role in the diets of omnivorous carp and tilapia species and terrestrial animals than in the diets of piscivorous fish. The proportion of fishmeal and alternative protein ingredients in aquafeeds depends on the nutritional requirements of the species, relative commodity prices, and the regulatory environment of production systems (e.g., Europe prohibits the use of rendered animal products in feeds).

Livestock, in particular, can substitute easily in and out of fishmeal according to price and preference. Many farmed fish have traditionally required the use of fishmeal and fish oil for nutritional and palatability reasons, whereas the same is not true for livestock. Nonetheless, the total amount of fishmeal used in livestock remains significant (1.6 mmt in 2007) despite low fishmeal and fish oil inclusion in diets (≤ 1%) because aggregate livestock production is large and continues to expand.

In contrast to overall protein needs, starch intake shows substantial variation

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[‡] The equation would change from that shown in Fig. 1 to $FI/FO = (RFE_{FM} + RFE_{FO})/2$, where RFE_{FM} is the same as in Fig. 1, and RFE_{FO} is calculated as $FCR \times Incl_{FO}/0.05$.

both among fishes and between livestock and fishes. The high basal metabolism of warm-blooded terrestrial animals requires greater food intake per unit growth as compared with cold-blooded animals, and this additional energy can be supplied by starch. However, intense genetic selection of broiler chickens has dramatically reduced their production cycle (hatch to market weight) and has thus resulted in lower starch intake compared with pigs. Indeed, farmed chickens now have a similar starch intake and overall efficiency in converting macronutrients to farmed weight gain as cold-blooded carp species.

Lipid requirements also show large variations among farmed fish species. As is characteristic of piscivorous fish species, Atlantic salmon metabolize fat very efficiently as an energy source and thus are fed relatively large amounts of lipids per unit of weight gain (Fig. 2). Salmon and trout are the most efficient converters of macronutrients to biomass, but they rely on energy-dense nutrients (lipids) and feeds made with high-quality ingredients. Even though the share of crop-based lipids incorporated in salmonid diets has been increasing fish oil remains a key ingredient (Table 1).

As consumption of salmon, trout, and marine fish species continues to expand globally, it will become even more important to increase the use of nonfish alternatives in aquafeeds. Feed management can help to reduce dependence on forage fisheries. Starter and fry feeds for salmonids and other marine species must contain high amounts of fishmeal to support growth and health, but levels can be progressively reduced once fish reach the juvenile and grow-out stages. Ninety-five percent of the feed eaten over a fish's lifetime is consumed during the juvenile and grow-out stages, so replacing fishmeal with alternatives at these stages has the greatest impact on reducing fishmeal use.

Alternatives to Forage Fish

Despite efforts to substitute away from fishmeal and fish oil in aquafeeds, many consumers, producers, purchasers, and policymakers remain unclear about the suitability and sustainability of alternatives. To be a viable alternative for fishmeal or fish oil, a candidate ingredient must possess certain characteristics, including nutritional suitability, ready availability, and ease of handling, shipping, storage, and use in feed production. In addition, feeds are selected on the basis of fish health and performance, consumer acceptance, minimal pollution and ecosystem stress, and human health benefits. Finally, competitive pricing is essential for the adoption of nonfish alternatives in feeds. Between mid-2005 and mid-2008, the prices of fishmeal and fish oil rose 50% and 130%, respectively (ref. 15 and Fig. S4). Greatly expanded demand from China, in particular, contributed to a rapid run-up in fishmeal and fish oil prices in 2006–2007 and, in turn, to a decline in fishmeal and fish oil inclusion rates in aqua and livestock feeds. Crop prices also rose sharply in 2007 to mid-2008 and then fell steeply with the global economic crisis. The recent price environment for fish and nonfish feed ingredients can be described as one of substantial volatility. However, given limited supply and increasing demand, the long-term outlook appears to be one of rising fishmeal and fish oil prices, a trend that could facilitate the substitution of nonfish alternatives, depending on relative price trends.

Terrestrial Plant-Based Proteins. Using plant-based proteins in aquaculture feeds requires that the ingredients possess certain nutritional characteristics, such as low levels of fiber, starch (especially nonsoluble carbohydrates), and antinutrients. They must also contain a relatively high protein content, favorable amino acid profile, high nutrient digestibility, and reasonable palatability. The range of plant feedstuffs in aquafeeds currently includes barley, canola, corn, cottonseed, peas/lupins, soybeans, and wheat. Although some plant-derived ingredients, such as soy protein concentrate and wheat gluten, possess most of the desirable characteristics, historically their high price relative to fishmeal has precluded extensive use in most aquafeeds. With sharp increases in the relative price of fishmeal and fish oil in recent years (see Fig. S5), however, these refined plant feedstuffs are now more economical.

Relative to fishmeal, plant feedstuffs generally have more indigestible organic matter, in the form of insoluble carbohydrates and fiber, leading to higher levels of fish excretion and waste. In addition, certain minerals in plant products, such as phosphorus, have limited uptake in fish. Recent advances in fish nutrition, feeding, and dietary manipulations have substantially reduced waste production and increased nutrient utilization and growth efficiency of farmed aquatic organisms (16). Improvements in this area continue to be made through classic breeding, transgenic manipulation, exogenous enzyme treatment [e.g., phytase in salmonid feed (17)], and postharvest processing technologies that enhance the quality of plant protein concentrates (18).

New plant-based products are also being developed, such as soybean, barley, and corn meals from coproducts of ethanol and biodiesel production. For example, the primary by-product of ethanol production is distiller's dried grains with soluble (DDGS) products. DDGS is a mixture of protein, fiber, and unfermentable carbohydrates and can be used in limited quantities as a feed ingredient for omnivorous farmed fish. However, the high fiber content and adverse palatability of DDGS limit its use in feeds for many species. Because the fiber in DDGS is not digestible by fish, adding DDGS to fish feeds increases fecal losses and thus ecosystem impacts of aquaculture (19, 20). The biofuel industry is currently developing new single-cell (yeast) products that are higher in protein than DDGS products and potentially more suitable as aquaculture feeds.

In addition, advanced genetics and genomics tools are being used to develop modified strains of aquatic organisms that can tolerate higher levels of plant feedstuffs in the diet. However, the evaluation of genotype by diet interactions in aquaculture species for specific dietary components has, to date, been limited to a few species, such as sea bream, rainbow trout, and Atlantic salmon (21, 22). Most other aquaculture species have more recently become domesticated, and their physiology and metabolism vary substantially.

Even without improved genetic lines of plant feedstuffs and fish, there are a variety of dietary manipulations that have proven effective in increasing the utilization of plant feedstuffs in aquafeeds. These include blending complementary feedstuffs to achieve amino acid profiles that better meet the metabolic requirements of the targeted species, or in some cases, supplementing commercially available forms of the most limiting amino acids, such as synthetic methionine analogs (23), various sulfur amino acid compounds (for methionine), or lysine HCl (24). Supplementing with nutrients or exogenous enzymes can also compensate for antinutritional factors and increase utilization of specific nutrient forms. Other diet supplements include, for example, prebiotics (not to be confused with therapeutic use of antibiotics) that are classified as nondigestible food ingredients that beneficially affect the host by stimulating growth and/or activity of certain health-promoting bacteria, such as *Lactobacillus* and *Bifidobacter* spp., in the intestine. Numerous studies of terrestrial animals have shown that altering the intestinal microbiota via prebiotics may achieve favorable effects such as enhancing growth, digestion, immunity, and disease resistance of the host organism. Although information on prebiotic use in aquatic organisms is limited to date, benefits such as increased feed utilization and disease resistance have been observed in fish and shrimp (25, 26).

Overall, the potential to substitute plant-based proteins into aquafeeds is high but will depend on their relative prices, availability, and palatability for individual species. Replacing half of the fishmeal in salmonid feeds with plant proteins is relatively simple, but further reductions are likely to result in lower growth rates, caused in part by deficiencies or imbalances in essential nutrients that have not yet been identified. Ongoing research will likely resolve this issue, but progress is expected to be slower than that required to reach the level of fishmeal replacement achieved to date.

Terrestrial Plant-Based Lipids. The past decade has seen an increase in the use of terrestrial plant oils, such as canola, soy, flax, and palm oils, to replace fish oil in aquafeeds. This replacement has been driven by the increasing cost of fish oil. For much of the 1980s–1990s, the price of fish oil was lower than that of vegetable oils, but fish oil has generally been more expensive since 2001 (see Fig. S4). Between 2006 and 2008, fish oil prices more than doubled to >\$1,800/mt. Although soy and palm oil prices also rose sharply in 2007, fish oil prices have remained relatively high.

Beyond the price advantage, terrestrial plant oils can be produced in sufficient quantities to meet growing aquaculture demand. The major sources of replacement for fish oil in Atlantic salmon diets include sunflower (27), linseed (28), canola/rapeseed (29), soybean (30), olive (29), and palm (31) oils. However, the replacement of fish oil by terrestrial plant oils also results in lower concentrations of the beneficial LC omega-3 fatty acids. Vegetable oils do not contain LC omega-3 (n-3) fatty acids and generally have high concentrations of the medium-chain oleic (18:1n-9), linoleic (18:2n-6), and in some instances α-linolenic acids (18:3n-3).[§] As a result, terrestrial plant oil and fish oil blends are commonly used in aquaculture diets, with the blending ratio determined by price, stage of production, and desired consumer outcomes. Currently, salmonid feeds contain blends of plant and fish oils during portions of the grow-out phase, followed by a switch to fish oil diets some months before harvest to increase LC-omega-3 oil levels in fillets.

The use of terrestrial plant oils containing the LC omega-3 oils' precursor, stearidonic acid (SDA, 18:4n-3), also shows promise for aquaculture feeds. For Atlantic salmon parr (freshwater phase), the use of an SDA oil has been demonstrated to maintain LC omega-3 oils at levels similar to that of salmon fed a fish oil diet (32). Although some fatty acid conversion occurs in salmon smolts (saltwater phase) and trout, the maintenance of LC omega-3 oil content is below that of the parr (33).

Another approach under development is the genetic modification of land plants, such as canola and soy, to produce LC omega-3 oils. Thus far, research has led to modest increases in LC omega-3 oils in a number of land plant species by using microbial gene insertions (34, 35). The achievement of sufficiently high concentrations is anticipated within a decade. The question then becomes one of consumer acceptance of genetically modified plant inputs in feeds.

The potential to expand the use of terrestrial plant-based lipids in the short to medium term is great. For example, experts estimate that 75% of dietary fish oil can be replaced by vegetable oils in Atlantic salmon without compromising growth, performance, or fish health as long as the LC omega-3 fatty acid requirements are met (30, 36). Such substitution has the potential to alleviate the aquaculture industry's pressures on forage fisheries in the future. It would also reduce human health concerns associated with the presence of dioxins and PCBs in fish feeds, which varies widely by source (3), because terrestrial plant oils do not contain harmful levels of PCBs and dioxins.

Single-Cell Protein and Oil. Single-cell oils (SCO), extracted from microorganisms grown under heterotrophic conditions, can also be rich in LC omega-3 oils. The whole-cell biomass or algal meal after extraction of these microorganisms is now used to feed larval stages of marine finfish, such as striped trumpeter, and is fed to chickens to enrich the eggs. One group of microorganisms (thraustochytrids) has also been successfully used in trials for use in the grow-out phase of Atlantic salmon, either as whole-cell biomass or the extracted SCO (37, 38). In those studies, fish oil was completely replaced by thraustochytrid oil in Atlantic salmon parr diets, resulting in comparable growth and fish health while increasing the concentration of DHA in fish flesh.

The high costs of SCO and/or biomass production in large-scale fermenters currently constrains their use in aquafeeds. SCO has been used successfully in shrimp culture (39), but the large quantity of oil required throughout the life history of salmonids and marine fish makes such a practice cost prohibitive. A potentially cost-effective approach is to use SCOs in finishing diets for the final 6–12 weeks of fish growth, which would enhance the LC omega-3 oil content and thus the value of the final product. This could be a practical intermediate strategy while other, cheaper sources of LC omega-3 oils, such as those derived from genetically modified land plants, are developed. There is also mounting interest by the biofuels industry to develop microalgae as a feedstock, which could help reduce production costs over time.

Rendered Terrestrial Animal Products. Another major source of fishmeal protein and potential lipid substitution is the suite of products rendered from terrestrial animals, such as meat and bone meal, feather meal, blood meal, and poultry by-product meal (40). Many of these products are readily available, economical sources of protein (41). Compared with vegetable proteins, animal by-product meals have a more complete amino acid profile, and some of them ingredients contain high levels of available lysine and phosphorous. The digestibility of these products has increased over the last 30 years to 80–90% because of improved processing techniques. They are significantly less expensive per kg of crude protein than fishmeal. For example, poultry by-product meal costs only \$0.79 per kg protein, whereas anchovy meal was \$1.13 per kg protein in July 2009 (see Table S2) (1, 42, 43). The main constraint on using rendered animal products in fish feeds is consumer acceptance. Most consumers are not aware that they are eating fish fed partially on animal products, but as more substitution in this direction occurs, the benefits of avoiding the use of forage fish will need to be weighed against the use of animal by-products in feeds.

Animal lipids are also inexpensive but they are high in saturated fats. Moreover, animal lipids have low digestibility at cold temperatures and must be blended with polyunsaturated fats to facilitate digestion. Using an animal–plant lipid blend during grow-out, in combination with finishing diets high in LC omega-3s, can help achieve the health benefits consumers desire in fish. Thus, the use of animal lipids in aquafeeds can contribute to a reduction

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[§] Fatty acid nomenclature: X:Yn-Z, where X is the number of carbon atoms, Y is the number of double bonds, and Z denotes the position of the first double bond from the terminal methyl end.

in the use of fish oil, but cannot provide a complete solution.

In the aftermath of bovine spongiform encephalopathy, an issue that is sometimes raised is the risk of disease transmission in using rendered animal by-products as feed ingredients. However, recent evidence suggests that the risk of transmissible spongiform encephalopathies (TSE) disease transmission via fish feeds is very remote. Prions, believed to be the causative infection agent of TSE, have been identified in various tissues of numerous fish species; however, fish prions and mammalian prions are genetically quite distinct (44). Multiple experiments have shown that prions from highly infective fresh brain tissues from mammals with TSE can be absorbed by the intestinal mucosa of fish and persist in these tissues for a few days. However, these prions do not cross the intestinal barrier and are rapidly cleared (45, 46). It is also important to note that a very large proportion of fish feeds are manufactured by extrusion, a high-temperature and -pressure cooking process. High-pressure cooking is one of the most effective techniques for deactivating defective prions. In the unlikely event that that the defective (potentially harmful) prions make their way into fish feeds, their number and infectivity potential would be almost completely destroyed by feed processing.

Seafood By-Products. The use of seafood by-products is another avenue for reducing aquaculture's dependence on forage fisheries. Globally, seafood processing by-products and by-catch together are estimated to be 25–30 mmt, approximately equivalent to the average landings of forage fish used to produce fishmeal and oil (47, 48). Seafood processing by-products represent a particularly attractive option for use in fish feeds; in 2002, an estimated 5.6 mmt of processing wastes (i.e., trimmings and rejects from food fish) were converted into fishmeal and oil, one-fifth of available by-product material (41). Using by-catch for feeds remains controversial because of its potentially deleterious effects on wild fisheries through relaxed by-catch regulations.

Despite the obvious potential for recovery of seafood processing by-products, formidable barriers exist to its utilization (49). Most importantly, by-products must be available in sufficient quantities and over a sufficient period to justify investing in the construction and operation of processing factories to convert them to meal and oil. Therefore, scaling up for processing remains a major constraint, with the exception of certain fishing ports such as western Dutch Harbor and Kodiak, Alaska.

The Alaskan pollock fishery is currently the largest source of seafood processing by-product meals. The nutritional quality of pollock by-product meals has been shown to be equal to that of the highest-grade fishmeal for shrimp (50) and marine fish (51). The ability of marine species to use feeds containing high levels of fisheries by-products is evidently greater than that of freshwater species (52). Fish meals produced from processing by-products differ in composition from those produced from whole fish, because a large proportion of the structural protein (i.e., muscle) is removed to produce fish fillets (53). Hence, the resulting meal has a lower protein content and higher ash (bone) content than conventional fishmeal. The ash fraction is rich in calcium and phosphorus, which can lead to antagonistic gastro-intestinal interactions causing zinc deficiency in freshwater farmed fish such as trout (54). Zinc deficiency affects growth and bone development, but more importantly, can cause cataracts (55). The problem is exacerbated in the presence of phytic acid, which is found in meals and concentrates made from grains and oilseeds (56). Thus, using high-ash fishmeal in conjunction with high levels of plant protein concentrates in aquafeeds is likely to cause zinc deficiency in farmed freshwater fish unless dietary zinc levels are increased by supplementation or steps are taken to mitigate phytic acid [e.g., phytase supplementation (17)]. The ash level in meals made from processing by-products can be reduced by mechanical screening of material after drying to reduce particle size (57) or by air classification. However, there are mechanical limits and yield constraints to how much bone can be removed with these methods.

One additional concern about the use of seafood processing wastes is that contaminants in the oil (PCBs, dioxins) of seafood by-products have the potential to bioaccumulate in farmed fish (3). The need to monitor this highly variable source of feed can act as an investment disincentive to feed producers. But if the scarcity of other feed sources increases the relative value of using seafood by-products in aquafeed, significant investments in solving the issues of contaminants, ash concentrations, and production scale are likely to be made.[¶]

Krill. The effects of the increasing demand for fishmeal and fish oil on wild fisheries is most likely to be felt at the margins, that is, in the few fisheries that are not fully used because of cost constraints. Krill is the single largest "underutilized" commercial marine resource remaining, so-called because the regulatory catch quota for the global industry is nearly 6 mmt while current total harvest is <1 mmt. Several species of krill, especially Southern Ocean *Euphausia superba*, have the potential to provide significant quantities of high-quality protein, lipids, and other nutrients (59, 60). The Southern Ocean krill is an abundant organism in Antarctic waters, with aggregate krill biomass estimated at up to 700 mmt (3). The global krill harvest peaked in the mid-1980s and then declined, settling at 100,000 to 150,000 mt per year for more than a decade. Because of renewed interest, the catch has increased again in recent years, with the annual harvest expected to double in the near future to 750,000 mt or more. One krill harvesting and biotechnology company from Norway, Aker BioMarine, is currently seeking Marine Stewardship Council certification for harvesting krill in the Atlantic sector of the Southern Ocean. The company plans to use krill in pharmaceutical and nutraceutical products and aquaculture feeds (ref. 61 and www.msc.org/track-a-fishery/in-assessment/southern-ocean/aker-biomarine-antarctic-krill).

Constraints on expanding krill use significantly in feeds include product variability, high perishability, and potentially serious ecosystem impacts. Krill contain LC omega-3s and significant amounts of phospholipids and antioxidants such as the carotenoid astaxanthin. The potential health benefits from these attributes are being marketed in various forms of krill oil products. However, the fatty acid profile of krill oil can vary by as much as twofold depending on the region, season of harvest, and interannual variability (62, 63). Moreover, Southern Ocean krill are highly perishable because of autolytic enzymes (64), and the highly unsaturated fatty acids are prone to rapid oxidation (65). Suitable collection, storage, transport, and processing conditions are needed to prevent or minimize oil and meal degradation (66).

Krill is at the base of the Southern Ocean food web and is also particularly sensitive to environmental variables, including climate change (67, 68). In some regions, considerable overlap exists between the krill fishery and the foraging ranges of land-based predators, such as penguins (69), which cannot move readily to new feeding areas. Local krill

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[¶] One study of fish meals made from by-products of the Alaska fishing industry revealed no detectable levels of PCBs or other contaminants (58).

depletion caused by fishing could also significantly reduce the food resources of other predators, such as seals and whales (70). Unfortunately, existing data on krill abundance and population variables are not sufficient to establish precautionary management of the krill fishery and its effect on the Antarctic ecosystem. Considerable care will thus be needed in setting local catch limits for krill harvest to protect key predators and other animals in the Southern Ocean ecosystem, and the Commission for the Conservation of Antarctic Marine Living Resources is trying to develop data-driven procedures to achieve this.

The Path Forward

For the aquaculture sector as a whole, the ratio of wild fish-in to farmed fish-out based on feed ingredients has fallen well below one (see Fig. S1). However, aquaculture's share of global fishmeal and fish oil consumption has risen substantially, as greater amounts of fishmeal are fed to omnivorous species, and high levels of fish oil are used to provide LC omega-3 oils in farmed fish. Our analysis shows that aquaculture's consumption of fish oil, in particular, is likely to determine the sector's absolute demand for marine resources, and hence, the sector's role in conserving or depleting wild fisheries in the future.

Because the biggest gains in reducing forage fish in feeds will come from lowering inclusion of fish oil (as opposed to fishmeal), there are two main avenues to future success: the acceptance of terrestrial plant LC omega-3 oils and the commercial development of SCOs. SCOs show great promise for reducing dependence on wild fisheries. They could provide 100% replacement of fish oils with LC omega-3s in the future, but their high cost of production makes them infeasible commercially for salmonids and marine finfish. This constraint could be alleviated through synergies with the biofuels sector if the high costs of production were to be concentrated in research and development (R&D) rather than in run-of-the-mill production. That is, biofuels could provide the push to develop and solidify the technology, and aquaculture could provide the market for such products.[‖] In the near term, using minimal levels of SCOs or fish oil during grow-out and only bumping up fish oil inclusion during the finishing stage is an important way to reduce the total amount of fish oil needed without major innovations in technology and new feed ingredients while still maintaining human health benefits of LC omega-3s in farmed fish products.

Ongoing progress in developing alternatives to fishmeal and fish oil in aquafeeds, especially terrestrial plant proteins and oils, animal by-products, and SCOs, will also help reduce aquaculture's pressure on marine resources. The main constraints include consumer acceptance, government policy in the case of using rendered animal products in the European Union, and high R&D and production costs for some technologies. The willingness of consumers and retailers to purchase farmed seafood that is fed diets containing recycled animal protein and oil or genetically modified plant oils remains in question. Our view is that consumer acceptance will be less problematic for genetically modified plant meals and oils than for animal by-products, as long as the genetically modified products are feedstuffs and not the final animal product. Most terrestrial animal feeds using soy products already contain genetic modification, with the exception of organic-labeled products.

Over the longer run, incentives will be needed to encourage technological development of nonforage fish inputs in feeds. A key question is whether the push should come from market incentives and regulation of the aquaculture industry (e.g., legislating certain requirements on the use of fishmeal and fish oil in feeds, as in California) or regulation of the fisheries sector. Continued pressure on forage fisheries will be inevitable, given expected growth in aquaculture, livestock, functional foods, and pharmaceuticals targeted at LC omega-3 products (see *SI Text*). With growing demand for animal feeds worldwide, particularly in Asia, where incomes and consumption of meat and higher-value fish products have been expanding in recent decades, effective regulation of global forage fish supplies and trash fish consumption is critical. The combination of demand-side regulation on feeds and supply-side management of forage fisheries could help create appropriate incentives for sustainable growth in the aquaculture sector. The key to supply-side management will be to factor in ecosystem needs; that is, forage fish and krill should be conserved for food web support, not just targeted for human catch at the maximum sustainable yield. This point is particularly important given the uncertain impacts of climate change on forage fisheries in the future.

In a globalized economy, price signals will provide the best inducement for technological and management change in the use of fishmeal and fish oil in feeds. But certain costs, particularly to ecosystems, are not priced in the market and require policy intervention to avoid. The strongest forms of intervention will be those that improve accountability of feed ingredient sourcing and encourage substitution away from fishmeal and fish oil consumption. With appropriate price signals, the aquaculture industry has the opportunity to benefit from a wealth of new feed technologies to reduce its dependence on forage fisheries. The trickiest part of the equation is the extreme volatility of all commodity prices in recent years, creating disincentives to long-term ingredient purchasing and systematic changes in feed formulations. By taking action now to implement the right policy interventions, one can only hope that by 2015 the transition toward alternatives will be well underway. If so, it is likely that a consensus will emerge that aquaculture is aiding the ocean, not depleting it.

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[‖] A recent example is Cyanotech in Hawaii, which provided SCO products rich in astaxanthin for both human consumption and animal feeds, but has recently stopped production of animal feed supplements to focus entirely on human supplements.

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